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Ralf Riedel

Barry A. Costa-Pierce

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Feeding Ecology of Salton Sea Tilapia (*Oreochromis* spp.)

Ralf Riedel¹

*Gulf Coast Geospatial Center College of Marine Sciences University of
Southern Mississippi Ocean Springs, Mississippi 39564*

Barry A. Costa-Pierce

*Rhode Island Sea Grant College Program, Department of Fisheries, Animal
and Veterinary Science, University of Rhode Island, Narragansett Bay Campus,
Narragansett, Rhode Island 02882-1197*

Abstract.—We investigated the feeding ecology of tilapia (*Oreochromis* spp) in the Salton Sea. Stomachs and intestines were sampled at each season. Fish foraged at the surface during the summer when dissolved oxygen was low. The proportion of plant materials in fish stomachs was higher at river mouth areas. Diatoms dominated the phytoplankton; rotifers were dominant during the spring and summer; copepods were dominant during the fall; barnacle larvae dominant during the winter. Pile worms (*Neanthes succinea*) were present throughout the year. Feeding activity was reduced in the summer, when dissolved oxygen was low and water temperature high.

Intra-specific feeding plasticity is widely recognized in fishes (Wootton 1998) and is a function of environmental factors (Fryer and Iles 1969). Feeding strategies of cichlids are diverse and highly adapted to exploit a variety of niches (Fryer and Iles 1972; Maitipe and De Silva, 1985; Bowen and Allanson 1982). Tilapia are the most widely distributed exotic fish worldwide (Lowe-McConnell 1975; Bowen and Allanson 1982) because of their importance in aquaculture (Costa-Pierce and Rakocy 1997, 2000). The success of tilapia invasions is in part due to their ability to respond quickly to environmental changes by varying life history traits (Bruton and Allanson 1974; Noakes and Balon 1982) and exploiting multiple trophic levels (Fryer and Iles, 1969; Bowen, 1982).

Feeding patterns in the Mozambique tilapia (*O. mossambicus*) may be a function of ontogeny and environment (Bowen and Allanson 1982). Mozambique tilapia in Lake Sibaya, South Africa, are known to be detritivorous and inhabit shallow areas in the juvenile phase and deep areas during adulthood (Brutton and Bolt 1975; Bowen 1979). Juvenile tilapia select the inshore areas in Lake Sibaya to seek refuge from predators (Bowen and Allanson 1982) and to take advantage of the more nutritious detrital aggregate (Bowen 1979). The Mozambique tilapia also has the ability to feed on plants and algae (Maitipe and De Silva 1985; Bowen 1982; DeSilva et al. 1984; Khallaf and Alme-na-ei 1987; Beveridge and McAndrew 2000). Mozambique tilapia can digest cellulose in addition to microbial and particulate matter in sediments due to high stomach acidity, which may reach

¹ Corresponding author: ralf.riedel@usm.edu

a pH of less than 1 (Dempster et al. 1995). Tilapia have also been known to feed selectively on animal matter (De Silva et al. 1984).

The Salton Sea is a 980 km², closed basin salt lake in the Sonoran Desert of southeastern California. The high salinity (44 g/L) and frequent wind-driven summer deoxygenation events of the lake make it an extreme environment conducive to unique behavioral adaptations in fish. Over 70 species of marine fish have been introduced starting in 1929 (Walker et al. 1961) and over 30 species have been introduced in major numbers (more than 50 fish). Major introductions were done between 1950 and 1956 into the Salton Sea from Mexico's Gulf of California (Walker et al. 1961) from which the orangemouth corvina (*Cynoscion xanthulus*, Jordan and Gilbert), Gulf croaker (*Bairdiella icistia*, Jordan and Gilbert) and sargo (*Anisotremus davidsoni*, Steindachner) established and flourished. During the late 1960s a hybrid tilapia (*Oreochromis mossambicus* Linnaeus × *O. urolepis hornorum* Linnaeus) invaded the lake (Costa-Pierce and Doyle, 1997) and became the dominant species (Costa-Pierce and Riedel 2000; Riedel et al. 2002).

Because the Salton Sea tilapia have higher growth rates than conspecifics in other systems (Riedel et al. 2002), nutritional constraints may not exist. Riedel et al. (2002) show evidence that the Salton Sea is a productive lake for tilapia, despite high summer water temperatures (over 32°C), frequent wind-driven anoxia over large areas, and high salinities. We investigated the feeding of Salton Sea tilapia to determine the possible reason for the high tilapia growth rates and production in the Salton Sea and to describe tilapia feeding ecology in this stressful environment.

Methods

Tilapia feeding was investigated by measuring stomach acidity, verifying the color of intestinal material, and determining stomach contents and fullness. Plankton samples were taken at the Salton Sea during the summer, spring, and winter to provide an estimate of food availability for tilapia. One hundred and fifty two fish were collected in the spring (43 fish), summer (38 fish), fall (38 fish), and winter (33 fish) from five stations at river mouth, nearshore, and pelagic areas (Figure 1) to assess feeding patterns according to seasons and sampling areas. Fish collections were done with multipanel, multimesh gill nets and plankton collections with a 40 µm mesh net.

Stomach acidity was measured at all seasons with an Orion micro-combination pH glass electrode model 9802BN. The acidity from the upper, mid, and lower sections of the stomach was measured within 1 h of capture from five randomly selected fish at all stations. After the measurements, all stomach contents were transferred to glass vials containing 10% buffered formalin and given a unique identification code. Stomach contents and plankton samples were filtered out of the formalin solution in laboratory using a 40 µm mesh and transferred to 75% ethanol. Stomach fullness was estimated from the difference between the weight of the full and empty stomach. At one station only (Figure 1), one gillnet was set for one hour at dawn, mid-morning, mid-afternoon, dusk, and night to investigate diel cycles in feeding, using stomach acidity as a proxy.

The color of the intestinal contents was determined within 3 h of capture to estimate the degree of food assimilation of ingested material (Moriarty 1973). Intestinal material was identified as either green, indicating poor assimilation, or

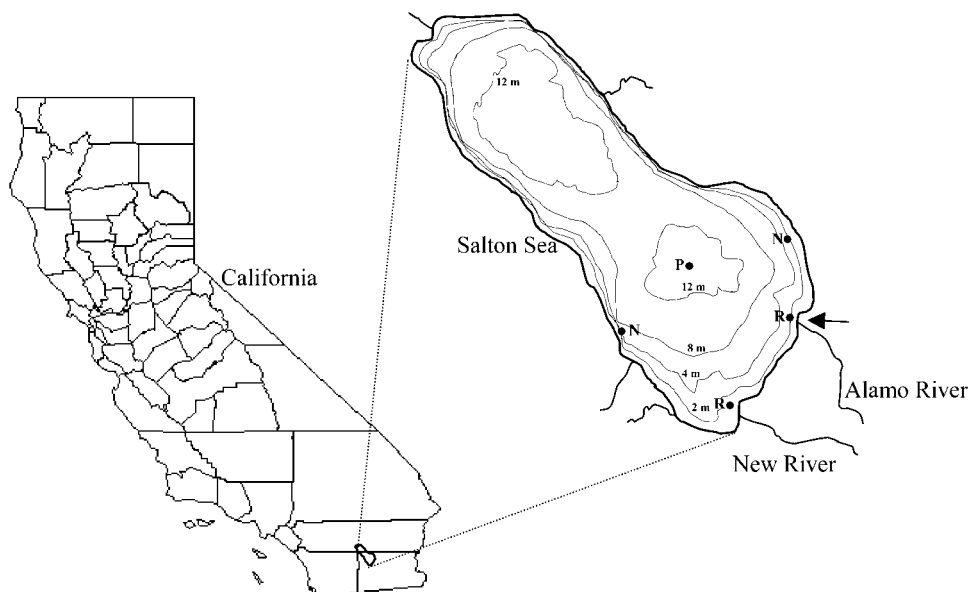


Fig. 1. Sampling sites at the Salton Sea. R—river mouth; N—nearshore; P—pelagic. Arrow indicates station where data were collected for assessing diel patterns in tilapia stomach acidity.

brown, for well assimilated food. No identification of organisms from intestines was attempted because of the advanced stage of digestion.

Stomach contents were grouped into sediment, plant material (macrophytes only), and Salton Sea biota. Sediment comprised sand, clay, and microbial organisms (not identified) and was used as a surrogate for determining foraging location within the water column. Macrophytes drift into the Salton Sea from land via the incoming tributaries. Macrophytes were considered because they are a potentially important tilapia food source, especially in the river mouth area. Salton Sea taxa were grouped further into benthos, zooplankton, and phytoplankton. Zooplankton were barnacles (planktonic stages of *Balanus amphitrite*), copepods (mostly *Cyclopods* spp), and rotifers (mostly *Brachionus* spp). Nematodes (mostly *Spilophorella* spp), ciliates, and pile worms (*Neanthes succinea*) were the benthic group. Phytoplankton consisted of dinoflagellates and diatoms. Groups of organisms other than the above were observed, but not analyzed due to low (< 1%) frequency of occurrence. Percentages based on numbers of organisms within taxa were defined for analyses within those groups for each stomach. Analyses of seasonal and spatial variation in feeding were done independently for all groups.

Percentages within taxa were averaged over individual fish to show taxa relative abundances according to space and season. Percentages, therefore, did not necessarily add to 100%. As a hypothetical example, if one fish had 100% of diatoms and another an empty stomach, the stomach content proportion was 50% diatoms for both fish taken together. The same rationale applies to proportions within groups. Because we report proportions of numbers, the often large abundance of phytoplankton would overwhelm all other taxa if no grouping was defined, overestimating the importance of abundant taxa and possibly precluding analyses for other groups of organisms.

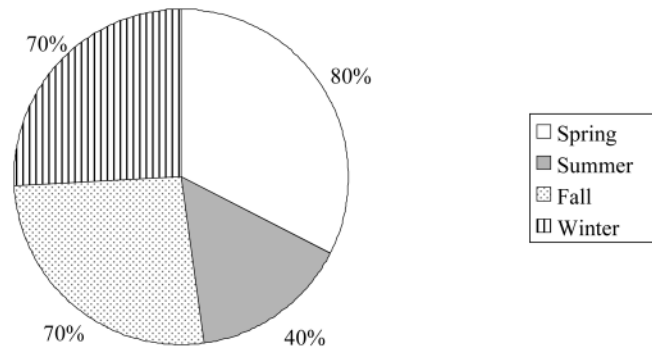


Fig. 2. Mean percentages of ingested sediment over all stations by season present in tilapia stomachs sampled at the Salton Sea. Spring $n = 43$, summer $n = 38$, fall $n = 38$, winter $n = 33$. Mean values were calculated from individual stomachs.

Because of heteroskedasticity in the data, proportions were analyzed using distribution-free statistical methods. Sediment and Salton Sea biota groups were analyzed for seasonal and spatial patterns. Kruskal-Wallis tests (Sheskin 2000) were used to assess seasonal and spatial patterns in feeding. Macrophytes were analyzed for spatial patterns only. The average percent of zooplankton in tilapia stomachs was compared with the percentages of taxa in plankton tows using a chi-square goodness-of-fit test (Sokal and Rohlf 1995) to estimate feeding electivity. Only barnacles, copepods, and rotifers were used because of the low occurrences of other taxa. Percent occurrence from plankton tows were the estimate for the expected value and the percentages from tilapia stomachs were the estimate for the observed value when conducting the chi-square test.

Feeding activity was estimated from the average acidity of the upper, mid, and lower section of each stomach (Moriarty 1973). A one-way analysis of variance (ANOVA) with color of intestinal material as the factor was used to assess the effect of stomach acidity on food assimilation. Diel and seasonal feeding activity was examined with a split-plot ANOVA (Winer *et al.* 1991), with time of day as the within factor and season as the between factor.

Results

The sediment proportion in stomachs was lowest during the summer (Figure 2; Kruskal-Wallis test statistic = 40.6, $p < 0.01$, 3 df). Macrophyte proportions were highest in river mouth areas (Figure 3; Kruskal-Wallis test statistic = 8.5, $p = 0.01$, 2 df). Diatoms were the dominant phytoplankton in the stomachs at all seasons and sampling areas. Diatom abundance was highest in the winter and spring and dinoflagellates highest in the spring (Table 1; Kruskal-Wallis test statistic = 14.3, $p < 0.01$, 3 df). Neither dinoflagellates nor diatoms varied in abundance according to sampling area.

The proportions of rotifers, copepods, and barnacles in stomachs varied with season (Figure 4; Kruskal-Wallis test statistic = 45.3 (barnacles), 74.0 (copepods), and 73.4 (rotifers), $p < 0.01$, 3 df). Rotifers were most common in the spring, copepods in the summer, and barnacles in the winter (Figure 4; Table 1). There was no evidence of a spatial pattern for either group. Chi-square tests indicated that there was no difference between the expected plankton percentages (plankton

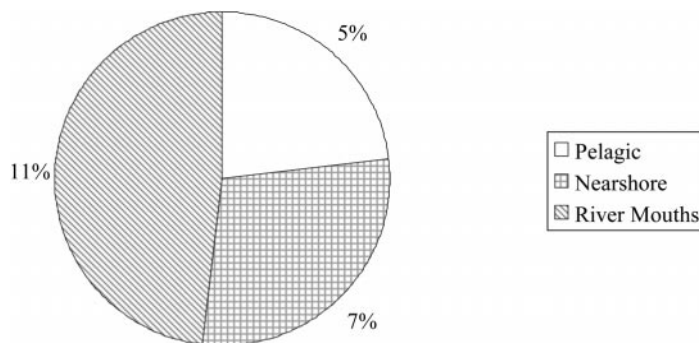


Fig. 3. Average percentages of ingested macrophytes by sampling area present in tilapia stomachs sampled at the Salton Sea. Pelagic $n = 11$, nearshore $n = 32$, river mouth $n = 109$. Mean values were calculated from individual stomachs.

tows) and the observed plankton percentages (tilapia stomachs) for barnacles, copepods, and rotifers during the summer ($p > 0.1$), fall ($p > 0.1$), and winter ($p > 0.1$; Figure 5).

Pile worms and nematodes were highest in the spring and fall (Table 1; Kruskal-Wallis test statistic = 11.1, $p = 0.01$ (pile worms), 29.6, $p < 0.01$ (nematodes), 3 df). Ciliates were highest during the summer (Kruskal-Wallis test statistic = 7.0, $p < 0.01$, 3 df). Pile worms in stomachs were more abundant at the river mouths (Table 1; Kruskal-Wallis test statistic = 7.0, $p = 0.03$, 2 df).

There was no pattern between intestinal color and stomach acidity nor was there evidence of stomach acidity varying according to time of day. Fisher's LSD post-hoc groupings were spring-summer and fall-winter (Figure 6). Stomach acidities were lower during the fall-winter period compared with the spring-summer period (Figure 6; split-plot ANOVA, $p = 0.02$ for factor season, 104 error df).

Discussion

Our observations show that the summer at the Salton Sea is a stressful period for tilapia. We commonly observed tilapia in the summer gulping air for oxygen and spending most of their time at the surface (Costa-Pierce and Riedel 2000; Riedel *et al.* 2002). Water temperature often surpasses 32°C and oxygen intermittently drops to zero over large areas during that season. We do not, however, exclude the winter from also being a stressful period for tilapia because water temperatures during winter may drop to their minimum lethal limit (Costa-Pierce and Riedel 2000).

The seasonal variation of the sediment quantity in tilapia stomachs indicates that fish spend the least amount of time foraging at the bottom during the summer. The presence of sediment in tilapia stomachs during the summer is indicative that fish can use detritus, despite anoxia at the bottom. Salton Sea tilapia in the summer may venture to the bottom to feed on detritus in the nearshore and quickly return to the surface for oxygen. Tilapia move toward the shore during warm months (Riedel and Costa-Pierce 2002; Costa-Pierce and Riedel 2000), possibly to take advantage of detritus when in shallow water.

Another potentially important food source in the summer are the macrophytes drifting into the Salton Sea from the surrounding tributaries. Even though tilapia

Table 1. Mean proportion (coefficient of variation; standard deviation/mean) of taxa identified from stomach contents. Mean proportions were calculated separately for phytoplankton, zooplankton, and benthos. Taxa are grouped by season and sampling area (R — river mouth; N — nearshore; P — pelagic). X — no fish sampled; numbers in parenthesis are quantity of stomachs analyzed (n).

	Spring			Summer			Fall			Winter		
	n = R (29)	N (10)	P (4)	R (32)	N (6)	P (0)	R (24)	N (12)	P (2)	R (24)	N (4)	P (5)
Phytoplankton												
Diatoms	0.93 (3.16)	0.43 (1.17)	0.25 (2.00)	0.35 (1.36)	0.33 (1.55)	X	0.42 (1.21)	0.67 (0.74)	0	0.50 (1.02)	0.75 (0.67)	0.20 (2.24)
Dinoflagellates	0	0.07 (3.16)	0	0	0	X	0	0	0	0	0	0
Zooplankton												
Barnacles	0.39 (0.84)	0.06 (2.63)	0.09 (1.85)	0 (5.60)	0	X	0 (4.70)	0.02 (3.28)	0	0.50 (0.96)	0.98 (0.02)	0.24 (1.81)
Copepods	0.08 (2.40)	0	0 (2.00)	0.23 (0.93)	0.24 (0.94)	X	0.78 (0.41)	0.53 (0.57)	0.82 (0.32)	0.09 (3.00)	0.02 (1.16)	0.04 (2.24)
Rotifers	0.38 (0.84)	0.34 (1.35)	0.74 (0.67)	0.75 (0.33)	0.86 (0.14)	X	0.12 (1.80)	0.28 (0.84)	0.18 (1.41)	0.02 (4.90)	0	0.12 (2.24)
Amphipods	0	0	0	0	0	X	0	0	0	0.01 (4.90)	0	0
Cladocera	0.02 (2.79)	0 (3.16)	0 (2.00)	0	0	X	0.04 (4.90)	0	0	0	0	0
Insects	0.01 (3.78)	0 (3.16)	0.17 (1.98)	0	0	X	0 (3.70)	0	0	0.01 (4.90)	0	0
Benthos												
Nematodes	0.29 (1.43)	0.78 (0.28)	0.85 (0.07)	0 (4.65)	0.03 (2.45)	X	0.58 (0.83)	0.50 (1.01)	0.25 (1.41)	0.36 (1.26)	0.01 (1.70)	0.20 (2.24)
Ciliates	0	0	0	0.62 (0.79)	0.54 (0.84)	X	0	0	0	0.04 (4.90)	0.71 (0.67)	0
Pile Worms	0.31 (1.32)	0.22 (1.00)	0.13 (0.49)	0.06 (3.93)	0.26 (1.61)	X	0.15 (2.23)	0.41 (1.21)	0.75 (0.47)	0.22 (1.74)	0.03 (0.85)	0
Ostracods	0.02 (5.39)	0	0	0.03 (5.66)	0	X	0.02 (3.50)	0	0	0	0	0

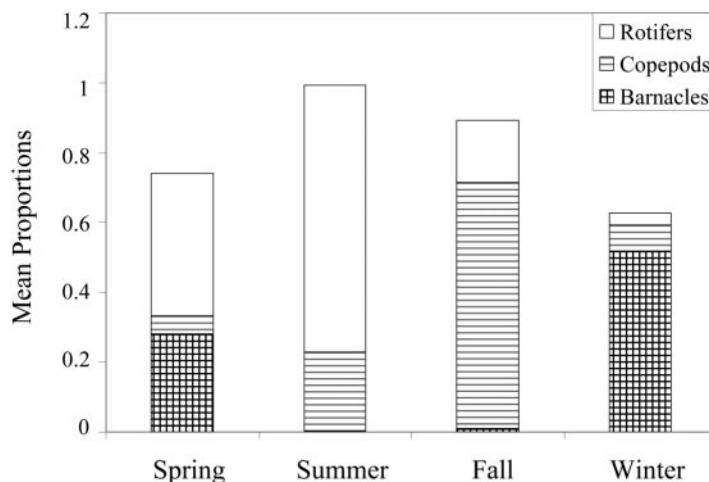


Fig. 4. Mean percentages over sampling areas of most frequent zooplankton in the diet of tilapia sampled at the Salton Sea. Differences in mean percentages by sampling area were not statistically significant. Spring $n = 43$, summer $n = 38$, fall $n = 38$, winter $n = 33$.

are not obligate herbivores, the high stomach acidity make tilapia an opportunistic herbivore. The digestibility of plant material in tilapia is not as high as that for true herbivores such as common carp (*Cyprinus carpio*), but high enough to provide some nutritional benefit (De Silva and Perera 1983). The highest concentration of tilapia in the summer is within the mixing zones between the river mouths and the Salton Sea proper (Riedel and Costa-Pierce 2002; Costa-Pierce and Riedel 2000). Fish seek the lower temperatures and higher dissolved oxygen at those locations. Tilapia may also prefer the river mouths because of the added benefit of macrophyte drift.

The importance of the phytoplankton to Salton Sea tilapia may have been underestimated because most phytoplankton cells may have been lost during our filtration or not captured during our plankton tows, due to the large mesh size we used. Our results, however, for the larger phytoplankton show that diatoms are the most important food item. The abundance of diatoms at the Salton Sea declines during the summer (Carpelan 1961a). Similarly, diatoms were less abundant in tilapia stomachs during that season. The proportions of barnacles, copepods, and rotifers in fish stomachs correlated well with their proportions in the water column and with the seasonal abundance patterns described in other studies (Carpelan 1961b; Tiffany et al. 2002). Tilapia species have been known to be unselective feeders (Beveridge et al. 1989). The close agreement between taxa in fish stomachs and taxa in the water column is evidence for low electivity for Salton Sea tilapia when feeding within the water column.

Pile worms become restricted to shallow areas of the Salton Sea in the summer due to anoxia and recolonize deeper areas in the fall and winter (Detwiler et al. 2002). Pile worms in tilapia stomachs increased during the recolonization period, indicating the importance of this food item for tilapia. Ciliates and nematodes were observed in tilapia stomachs and may contribute to the nutritional value of sediment, but are likely not as important as pile worms due to their small sizes.

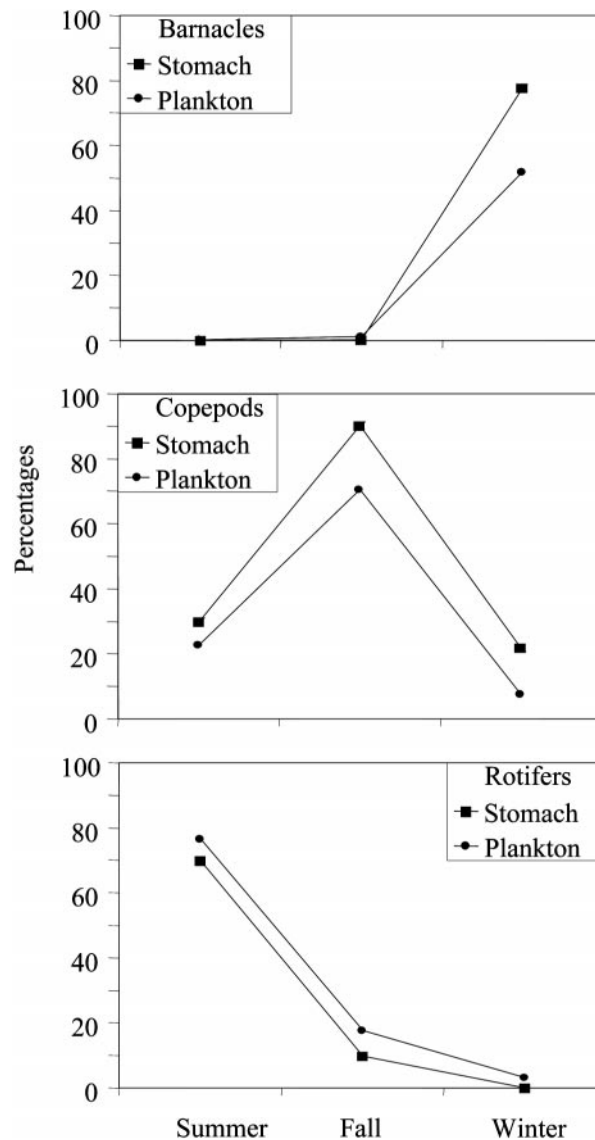


Fig. 5. Contrast between frequency of barnacles, copepods, and rotifers from tilapia stomachs and from the Salton Sea water column during the summer, fall and winter, 2000. Chi-square of summer = 0.04 (ns), fall and winter = 0.18 (ns); Observed—percentages in tilapia stomachs, Expected—percentages in the water column from plankton tows.

The higher occurrence of pile worms in tilapia stomachs from the river mouths may be due to the higher aeration of the sediment at that area.

We did not observe a pattern in the color of intestinal material possibly because tilapia do not feed exclusively on plants. Epiphytic algae and aquatic vegetation are low at the Salton Sea, except for macrophytes drifting from the incoming tributaries. Salton Sea tilapia, including specimens at the river mouths, rely mostly

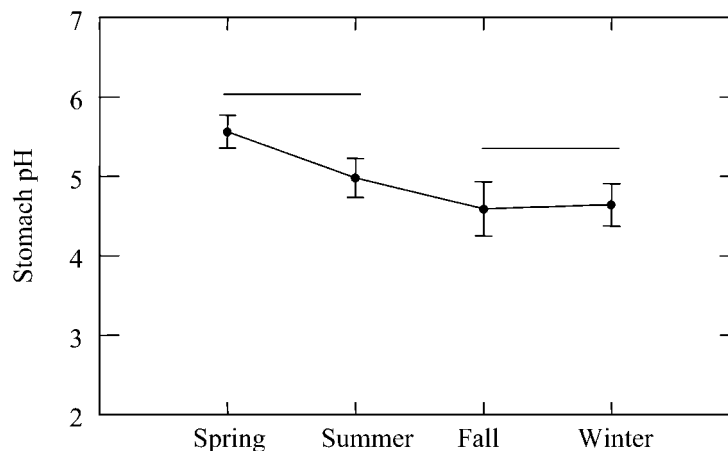


Fig. 6. Mean \pm SEM stomach acidity by season for tilapia stomachs at the Salton Sea. Horizontal bars indicate analysis of variance post-hoc groupings (Fisher's LSD, $p < 0.05$; $p = 0.02$ for factor season, 104 df).

on plankton and benthic organisms for food, keeping the color of intestinal material brown, even if food is not digested.

Tilapia at the Salton Sea reproduce from the spring to the end of summer (Riedel *et al.* 2002). According to our stomach acidity data, tilapia feeding increases during fall and winter. In the spring, tilapia are getting ready to reproduce and in the summer tilapia are stressed from anoxia and high temperatures. The critical period for growth may be a short period between the fall and winter before temperatures decrease below suboptimal, and the early spring, before reproduction. During those periods, we observed many fish stomachs full with adult pile worms, further evidence of the importance of this polychaete in determining tilapia condition and supporting its population.

The Salton Sea recently experienced massive bird mortalities (Tetra Tech 2000). Among the culprits is a bacterium, *Clostridium botulinum*, which causes botulism in pelicans. Pelican mortality is highest during summer and is possibly mediated by tilapia. Pelicans feed on tilapia infected with the bacterium. Because the bacterium and its spore are inhibited from growing in acid environments (pH 4.6 or below), we hypothesize that *C. botulinum* should be more common in tilapia stomachs during the spring and summer, based on the patterns of tilapia stomach acidity found here (Figure 6).

The success of Salton Sea tilapia may be attributed to its high feeding plasticity. Fish derive nutritional value from plants and plankton in the summer, but rely mostly on the pile worms during the fall and winter, making those seasons critical for tilapia growth and production. Because of the predominance of pile worms in the sediments during the fall and winter (Detwiler *et al.* 2002), they are likely responsible for the high growth rates and production of Salton Sea tilapia.

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results do not necessarily reflect the views of the Agency. No official endorsement should be inferred.

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